normal imitation-related cortical activations in ASD with normal IQ are located mostly within the inferior frontal gyrus as opposed to the superior temporal sulcus and inferior parietal lobule (Nishitani et al. 2004). In light of these neurophysiological results, it may be that modularity of the MNS can account for differential language symptomatology, with Broca's area being the principal component of the system.

Blindness. Another pathological condition that may add some insight into the perspective offered by Arbib is congenital blindness. It has been suggested that congenitally blind individuals display autism-like characteristics (Hobson & Bishop 2003). For example, visually impaired children perform at lower levels than normal subjects on theory-of-mind tasks (Minter et al. 1998), and blind children are at an increased risk of meeting diagnostic criteria for autism (Brown et al. 1997). Interpretation of these data as suggesting a causal link between sensory deprivation and autism-like characteristics has been challenged (Baron-Cohen 2002), but they nevertheless bring to mind interesting questions regarding ASD, MN function, and language impairment.

Some blind children display fewer periods in which they direct language towards other children and are generally impaired in the social and pragmatic aspects of language (Hobson & Bishop 2003), reminiscent of individuals with ASD. In blind individuals, lack of visual input would derail the normal mechanism matching action perception and execution within the visual system. A motor resonance mechanism could still operate through the auditory modality (Kohler et al. 2002), but in an obviously limited manner due to lack of visual input.

Mechanisms of disorder. We have tried to describe two pathological conditions that offer insight into the role of the MNS in language/communication. We have showed that a breakdown in MN function may be associated with specific language impairments, most notably pragmatic speech. In contrast to the theory put forth by Arbib, these examples speak to the ontogeny, rather than the phylogeny, of language. Nevertheless, they share a striking similarity: the necessity of an adequately "evolved" (as Arbib puts it) MNS to develop the unique ability of human language. Although still speculative, the two conditions we have described suggest different mechanisms that may lead to MNS impairment and associated language deficits.

In the case of blindness, it may be that loss of visual input impairs the normal development of a motor resonance system, thereby leading to language/communication deficits. In that sense, it is an environmental factor that hinders adequate development of the MNS. In ASD, where genetic factors are an important part of the etiology, individuals may be born with a dysfunctional MNS, preventing normal language and social behavior. In that regard, it is tempting to look at the Forkhead box P2 (FOXP2) gene, located on chromosome 7q, which is believed to be implicated in the acquisition of language (Lai et al. 2001) and may be involved in the human properties of the MNS (Corballis 2004). Most evidence argues against a direct link between autism and FOXP2 (e.g., Newbury et al. 2002), but the idea that MN development may be genetically determined is an intriguing possibility that requires further investigation.

In summary, this commentary highlights the need to test Arbib's theory against various pathological conditions, either those specific to language (e.g., aphasia) or those which may be associated with MN dysfunction (autism, schizophrenia, Williams' syndrome). For example, one of the co-morbidities of specific language impairment (SLI) is motor impairment (Hill 2001), suggesting yet another association between motor skill and language dysfunction. It seems obvious to us that specific predictions of Arbib's model need to be tested this way, as direct evidence in support of some aspects of the theory is lacking.

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Language is fundamentally a social affair

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Abstract: Perhaps the greatest evolutionary advantage conferred by spoken language was its ability to communicate mentalistic concepts, rather than just extending the vocabulary of action already served by an imitation function. An appreciation that the mirror-neuron system served a simple mentalising function before gestural communication sets Arbib's theory in a more appropriate social cognitive context.

It may not be an obvious question to ask why spoken language should evolve from gestural communication, but it is an important one. Simply put, if gesture can be used to communicate effectively, why evolve speech? Why didn't we just evolve a complex gesturing language that did not require changes to the larynx? Arbib has presented a theory of language evolution but has omitted to discuss the selection pressures involved.

According to the Machiavellian intelligence hypothesis (Byrne & Whiten 1988; Whiten & Byrne 1997), the human brain evolved because of the selection pressure to develop cognitive capacities that facilitate social manoeuvring. This would also suggest that language evolved through the need to communicate mental states. The evolution of language would be driven primarily by the need to discuss matters such as loyalty, betrayal, forgiveness, and revenge. Arbib uses few examples to illustrate the content of the language he is discussing; he mentions gestures used to describe flying birds, hunters directing each other, the tastes of food, and the use of fire to cook meat. His argument seems to assume that speech and gesture are used to discuss the physical activities of daily living, rather than to express feelings, desires, or intentions, or to consider the thoughts of conspecifics.

Also, Arbib derives his model of imitation from that proposed by Byrne and Russon (1998) following their observations of leaf-folding by mountain gorillas. This is an imitative task that requires replicating the structural organisation of an action, rather than the mental states driving it. Communicating the knowledge inherent to this skill is a relatively straightforward matter using action demonstration, whereas to describe it using only speech would be more difficult. Conversely, communication concerning invisible mental states may lend itself more to speech than descriptive gesture. Consider for example, "John wrongly thinks that Bob is jealous of me," or, "you distract John whilst I plot revenge against Bob." It may be that in the discussion of invisible mental states, speech can add a valuable modality of communication, which may even supplant manual and facial gesture.

Arbib does not mention the possible role of the mirror-neuron system in mentalising, or the importance of this mentalising function in imitation. Imitation involves incorporating a novel action into a pre-existing behavioural repertoire (Whiten et al. 2004). It follows that for this to occur, the observed behaviour must be compared with the existing knowledge of the behaviour. Therefore, imitation requires more than remembering and then replicating the components and organisational structure of an action sequence. Rather, imitation requires that the observer draw on his or her own knowledge of an action exhibited by a model. This includes the observer's knowledge of the action's relationships to causes, beliefs, goals, desires, effects, and agency. Only then can the observer understand the role of the action in the model's behaviour.

Actions are therefore vehicles for the thoughts that shape them, in that thoughts are carried by actions from mind to mind. Both imitation and "simulation theory of mind" involve observing actions or behaviours from a stance of using self-knowledge to predict the mental states behind them (Meltzoff & Decety 2003). This means that both "theory of mind" and imitation depend on relating perceived actions to their motor counterparts (Meltzoff & Prinz 2002). The mirror-neuron system is the prime candidate to serve this function (Gallese & Goldman 1998), not as the only component, but by providing the original action-perception links that constitute the evolutionary origins and the developmental core for social cognitive growth. I suggest that it is the capacity of the mirror-neuron system to represent an observed action as if it were the behaviour associated with a self-generated mental state, thereby allowing for attribution of intention (and a secondary representational capacity; see Suddendorf & Whiten [2001]), rather than its capacity for coding an action's organisational structure, which enabled the mirror-neuron system to serve highly flexible imitation and praxis.

The neurodevelopmental disorder of autism is characterised by major developmental impairment of social cognitive ability, including imitative and mentalising abilities. Another characteristic feature, that is highly discriminative diagnostically, is the reduced use of all gestures, whether descriptive, instrumental, emphatic, or facial (Lord et al. 2000). This suggests that the neural system in humans serving gestural communication is knitted to that serving other social cognition (Williams et al. 2001). Whether dysfunctional mirror-neuron systems account for this symptom cluster is still a matter for research, but it seems unlikely that during evolution, language became more divorced from social cognitive systems once it became spoken. Indeed spoken language can become divorced from social cognition in autism, when it may be repetitive, stereotyped, and pragmatically impaired, such that its communicative function is severely impaired. If language did evolve only as Arbib describes, it could be impaired in a similar manner.

I suggest that the evolution of language from object-directed imitation would have been intimately tied to the evolution of social communication at the neural level. During early hominid evolution, the representations being pantomimed through gestural communication (including facial expression) would have been concerned with mental states, including feelings and desires. Facial and manual gestures were being used by individuals to express both their own feelings and what they thought others were feeling. The neural systems serving these functions would form the basis for the communication of more complex mental states, which would recruit vocal and auditory systems as well as semantic and planning structures in temporal and frontal lobes.

In summary, I suggest that mirror neurons first evolved within social cognitive neural systems to serve a mentalising function that was crucial to their praxic role in imitation and gestural communication. As the evolution of social language was driven through the need to convey and discuss invisible mental states, and these became increasingly complex, so a vocal-auditory modality became recruited as an increasingly valuable additional means of communication. This extended, rather than altered, the fundamentally social nature and function of language, and maintained its dependence upon social cognitive mechanisms such as secondary representation.

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The explanatory advantages of the holistic protolanguage model: The case of linguistic irregularity

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Abstract: Our tolerance for, and promotion of, linguistic irregularity is a key arbitrator between Arbib's proposal that holistic protolanguage preceded culturally imposed compositionality, and the standard view that discrete units with word-like properties came first. The former, coupled with needs-only analysis, neatly accounts for the second-order linguistic complexity that is rationalised as fuzzy grammaticality, subclass exception, and full irregularity.

Any model of language evolution must explain four basic things:

1. The interface between real-world semantics and the arbitrary phonetic medium: a difficult problem, particularly if subcortical reflex vocalisations are not the precursor of speech;
2. The capacity for fast and fluent formulations of phonological strings, since this has no obvious purpose beyond language itself (unless for display);
3. Our ability to express and understand messages that juxtapose many separate meaning features; and
4. Why languages appear to be unnecessarily complex, relative to the perceived underlying simple rule systems.

Arbib's integrated model offers an explanation for the first three by identifying manual dexterity and imitation, exapted for pantomimic communication, as the conduit between holistic message and oral articulation. Associating Broca's area first with grasping and imitation is much more satisfactory than attributing to it an a priori involvement in language that must then be independently explained. Indeed, in line with Arbib's section 8, neurolinguistic and clinical evidence strongly suggests that linguistic representation in the brain is mapped on the principle of functional motivation, so language operations are expected to be distributed according to their primary functions or derivation (Wray 2002a, Ch. 14).[1]

However, Arbib's model also indirectly offers an explanation for point 4. In Arbib's scenario, complex meaning existed in holistic expressions before there was a way of isolating and recombining units. The subsequent application of what Arbib terms "fractionation" ("segmentation" for Peters [1983], who identified the process in first language acquisition) is viewed as culturally rather than biologically determined, and consequently, piecemeal and circumstantial rather than uniform and universal.

On what basis should we favour this proposal over the standard alternative (e.g., Bickerton 1996), that there have always been discrete units with word-like properties, which became combinable to create meaning, first agrammatically (protolanguage) and later grammatically? First, we can note that attributing to our biologically modern ancestors a default capacity for holistic rather than compositional expression, begs the question: Where is that holistic foundation now? Wray (2002a) demonstrates that holistic processing, far from being peripheral and inconsequential, is in fact alive and well and motivating much of our everyday linguistic behaviour.[2]

But I want to focus mainly on one linguistic phenomenon that has long caused puzzlement and demanded much explanatory effort: irregularity. It is surely a necessary corollary of the standard view of language as an ab initio combinatory system that we are predisposed to orderliness, and that unnecessary complexity and irregularity are an aberrance to be minimised rather than promoted or protected. Hence, first, we should find that languages attempt to cleanse themselves of phonological and morphological exceptions, oddities in patterns of lexical collocation, grammatical restrictions of the sort that demand subcategorisations of word classes, and lexical gaps. For instance, we would expect the upgrading of adjective subsets that cannot occur predicatively (**The objection is principal*) and attributively (**the asleep boy*), and the filling of gaps in lexical sets, for example, *horror/horrid/horrify, terror/*terrid/terrify, candor/candid/*candify* (Chomsky 1965, p. 186). Such cleansing does not generally occur. Most irregularity is preserved intact from one generation to the next. Although regularisation does happen at the margins, it is balanced by the creation of new irregularities (see below).

Second, children acquiring an L1 that is fully regular and transparent, such as Esperanto, ought to do so efficiently and perfectly. However, they do not (Bergen 2001). Instead, they introduce (apparently permanently) irregularities and sub-patterns that render complex the simple system of the input.

Third, if native speakers naturally develop a full compositional